

The University of Chicago

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MICE

A DISSERTATION SUBMITTED TO THE
FACULTY OF THE DIVISION OF THE
BIOLOGICAL SCIENCES IN CANDIDACY FOR
THE DEGREE OF DOCTOR OF PHILOSOPHY

DEPARTMENT OF ZOOLOGY

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INTRODUCTION

The present study is devoted to the social relations between individual white mice caged together. It has, however, offered an opportunity for comparison with the analyses of other social hierarchies and is motivated by the suggestion of Allee (1935) that just as the digestive processes of fishes, ants, birds, and man are specialized developments from a commonly shared general physiology of digestion, so the social processes of diverse forms of animals are more or less intricate specialized developments from a common general sociology.

Schjelderup-Ebbe, whose pioneering work (1922) was a stimulus to other investigators, has studied the social organization of birds in more than fifty species. He states that in all of them despotic relations exist between individuals of a flock. The one member of a pair is always dominant and the other always subordinate, except on rare occasions when the order may be reversed through a decisive revolt.

Katz and Toll (1922) attempted to correlate the peck order and intelligence in a group of six hens. The hen at the top of the social order definitely gave the best performance in most of the various tests. But a correlation of the peck order and the test performance of the other five hens is much less obvious. More groups of chickens must be similarly studied before any reliable generalizations regarding the relation of peck order and intelligence of the chicken can be made.

Masure and Allee (1934a, b) studied the flock organization

¹ I am very grateful to Dr. W. C. Allee for suggesting this problem and for offering much inspiring and valuable advice.

of the common chicken, the pigeon, and the shell parakeet. They found essentially the same absolute peck right in the chicken as Schjelderup-Ebbe reported for all the birds he studied. In the pigeon and the shell parakeet, however, their results differ significantly. Instead of a "peck-right"—with the one animal always the undisputed victor and the other always the vanquished—they found a "peck-dominance" in which one member of a pair won the majority but not all of the contacts. They found no correlation in several groups of shell parakeets between peck order and maze performance (1936).

Murchison (1935a, b, c, d), studying six roosters and five hens, reported a correlation between: (1) peck order, (2) tread order, (3) relative amount of movement toward another bird in a runway, (4) social discrimination, and (5) the loss of body weight under conditions of mild starvation. Murchison, Pomerat, and Zarrow (1935) found no correlation between social order and the size of each bird or any of its organs. As Murchison well realized, a careful repetition of such experimental measurements on more groups of chickens is necessary to establish his conclusions.

Social organization among mammals is mentioned casually in many naturalistic accounts but relatively few careful observations on the social inter-reactions of these animals have been reported. Alverdes in *Social Life in the Animal World* (1927), Yerkes and Yerkes in *The Great Apes* (1929), Allee in *Animal Aggregations* (1931), and Zuckerman in *Social Life of Monkeys and Apes* (1932) give a good survey of our knowledge of this subject. All of these men, except Zuckerman, give a briefer and more recent account of this subject in their respective chapters in Murchison's *Handbook of Social Psychology* (1935).

Schjelderup-Ebbe (1925) lists seven species of domestic and numerous species of wild mammals in captivity that he has studied; his discussion of the social organization of these forms is exceedingly brief. According to him, the outward display of despotism in mammals may assume different forms in different species. In some it cannot be detected, except in the mating season or at feeding time. The social organization among mammals, he believes, is on a somewhat higher plane than that among

birds because of a greater degree of tolerance exhibited by the dominant toward the subordinate. He maintains, however, that here, as in birds, there are no two animals living together but that each "knows" which of the two is dominant and which is subordinate.

Yerkes and Yerkes (1935) report that dominance and subordination are evident in many groups of primates. As these authors point out, however, Carpenter (1934) in his study of the howler monkey apparently has discovered a notable exception to the dominance-subordination type of primate organization. The bands of the howler monkey seem to be organized along communal and coöperative lines, with no particular individual the dominant member of the group. Age, sex, size, vigor, alertness, resourcefulness, and temperamental characteristics, according to Yerkes and Yerkes, function as determiners of the order of dominance. Apparently, however, no quantitative study of the relative importance of these suggested determiners has been made. Maslow (1936) has attacked the problem of the rôle of dominance in the social and sexual behavior of infra-human primates.

Fighting among albino mice has been a common laboratory observation. This fighting tendency in the mouse offered an excellent opportunity to study dominance-subordination relationships in a simpler form than that found in species having a more complex social organization. The social hierarchy as observed in white mice has also been tested experimentally to find the possible correlations with various factors such as size, age, sex, familiarity of surroundings, and with the effect of blinding, castration, and partial starvation.

MATERIALS AND METHODS

The colony of mice used in the present investigation originated from a colony in the Hull Zoological Laboratory, which in turn had been started from a group of six male and twelve female albino mice bought at a local pet store. The first lot of breeding animals obtained from the Hull Laboratory and used for building up the colony for the present study had been inbred for at least

three generations. Later additional breeding mice were obtained from the same source to further increase the size of the colony; these had been line-bred. To develop and maintain a colony of several hundred mice, some breeding was carried on almost continually. Both brother-sister mating and less closely related mating occurred, but no other strain of mice was added. Pregnant females were isolated and the date of the birth of the litter was recorded.

The mice were kept in a windowless room in the Whitman Laboratory of Experimental Zoology. Ceiling lamps and desk lamps near the cages were used for light. The number of hours and the time of illumination were variable. Generally the lights were turned on for approximately two hours in the forenoon, two in the afternoon, and two in the evening. The temperature of the room ranged usually from 20° to 25°C., but for one period of six months it was around 16°C. and for another period of about three months it often reached 30° to 33°C. Almost all observations, however, were made when the temperature was around 23°C. Fresh air from the outside was circulated steadily through the room by an efficient ventilating system.

The animals were kept in galvanized wire cages. These were double-compartment cages with a removable metal partition. The inside measurements of each compartment were 10 by 10 inches and 7.25 inches high. The cage was equipped with a wire slide door and a raised wire bottom mesh and was set in a metal tray. A small amount of excelsior in one corner of the cage served as nesting material. Too much excelsior would enable the mice to escape the observer's view and so would hinder the observation of the inter-reactions of the animals.

Water and food were present practically at all times. The food consisted of a dry mixture of: six parts cracked wheat, thirteen parts rolled oats, one part powdered whole milk, by weight, and a small amount of cod liver oil. Lettuce was fed usually once a week.

Each male mouse was marked with two marks: (1) a yellow spot made with picric acid which served as a litter mark, and (2) a black spot made with Ursol D fur dye which served as the

individual mark. In this way each male could be readily distinguished from any other mouse in the colony. Females were marked individually with picric acid.

Observations of the fighting behavior began March, 1935, and continued, with interruptions during the summer months and for a few short periods at other times, up to April 20, 1937. Usually daily observations, including Sundays, were made from one to six hours per day, generally for one hour in the forenoon and one or two hours in the afternoon or evening.

The cages were arranged in two semi-circular rows—the one back and above the other—in front of the observer so that he could see the activity in every group of mice without changing his position. As many as thirty groups were watched at one time during the busiest part of this study. This was possible because fighting was usually scattered so that while it may have occurred in practically every pen in the course of an hour, conflict in several cages simultaneously was unusual. When the latter did occur it was sometimes impossible to record all of the fighting activities of each group. The daily record shows which animals were involved in fighting and the apparent outcome of each fight.

A "fight," as used in this study, is an encounter between two or more mice. It may vary in length of time from a fraction of a second to several minutes. In intensity it may vary from a mere snap or dart at an opponent to very severe biting. Both, or all animals may bite each other with apparently equal severity, or one animal may do all of the biting and the others give no resistance at all. In a great majority of the cases one animal actually bites another. In some few cases, however, the one animal may merely snap at another or follow it without getting a chance to bite. In some encounters the combatants fight with about equal severity and separate without either male showing any signs of defeat. Such fights are recorded as "no-decision" fights. One to many such unsettled encounters may occur between two animals before one of them is finally defeated. A defeat is indicated by the fact that the one mouse squeals and runs away from his opponent or at least fails to fight back when attacked.

Because fighting was much more common among males than among females or between members of both sexes, the emphasis of this study was placed on the social order among the males. The study of the females, however, was by no means neglected.

Studies of the behavior of more than 300 males and approximately 150 females, arranged in 85 groups of various sizes and composition, formed the basis of this report. Some cages contained only one litter, others several litters combined at various ages, and still others a mixture of individuals each of which came from a different litter. Some groups consisted of males only, others of both males and females. The more usual number of males in one cage was 3 to 6—the maximum, 9—and the number of both males and females in one pen was generally 4 to 8, seldom more than 10.

OBSERVATIONS

Types of social order

A survey of the records of the 85 groups of males observed daily clearly brings out the fact that the social hierarchy among males as expressed by their fighting behavior is by no means the same in all groups, or even in the same group all of the time. There is a continuous series of conditions that ranges all the way from complete, exclusive, and fierce domination of all other males in the pen by one mouse—sometimes resulting in the death of all but the despot—to no observed fighting. Dividing this continuous series into relatively few categories is admittedly an arbitrary procedure; as in many systems of classification, it is sometimes difficult to draw the different boundary lines. For convenience in describing the observations, however, the various conditions found among the males are classified into the following categories:

1. *Exclusive dominance* by one male of the group, without observed resistance from any of the other members.
2. *Dominance* by one male *with observed resistance* from one or more others.

- (a) Resistance with victory by the dominant animal.
The dominant mouse is at least once victorious over his fighting opponent and is not once defeated by him for that day.
- (b) No-decision resistance.
The dominant individual routs some subordinates but has only no-decision fights with one or more others that day.
- 3. *Linear order* of dominance, or *primary dominance* by one male and *secondary dominance* and even *tertiary dominance* by one or more others.
- 4. *Linear order with some resistance*; or primary dominance with resistance, and secondary dominance.
 - (a) Resistance with victory by the primary dominant.
 - (b) No-decision resistance.
- 5. *Equal dominance* by several males. Two dominants are regarded as equal if they defeat other males but not each other.
 - (a) No fighting between equals.
 - (b) No-decision combats between dominants.
- 6. *Unsettled dominance*. Each male that has been victorious in some encounters was in turn defeated in others that same day.
- 7. *No fighting*.

All of these types of conditions are illustrated diagrammatically in figure 1.

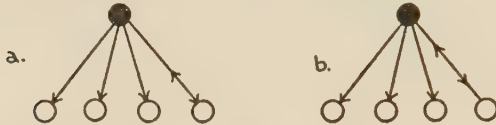
In some lots of males the same type of order was observed for many consecutive days, with each individual remaining in the same position in the hierarchy. In others the same type of order persists but dominance shifts from one individual to another. In others one condition may prevail for a considerable length of time and then give way to a new type of order which may persist for a while and in turn give way to another. In still other pens of males a different type of social hierarchy may be observed every day or two.

Rather than giving complete accounts of each group for the entire period of observation, the number of days each type of social order was recorded is summarized for each of the 85 pens of males. These data might have been put all in one table but they have been arranged in six tables both to facilitate reading and to emphasize that in some groups of mice one type of domi-

1. Exclusive dominance by one male.



2. Dominance with some resistance.



3. Linear order of dominance.



4. Linear order with resistance.



5. Equal dominance.



6. Unsettled dominance. 7. No fighting.



Legend

- → ○ = ● defeated ○ without resistance.
 ● ← ○ = ○ defeated ● but sometimes with resistance.
 ● ↔ ○ = fought with no decisive result.
 ○ ↔ ○ = fought with temporary alternating dominance.

FIG. 1. DIAGRAMS ILLUSTRATING REPRESENTATIVE TYPES OF FIGHTING RELATIONSHIPS AMONG MALE MICE

nance order was very conspicuous, while in others a different social hierarchy was most prominent. This series of tables is arranged as follows:

Table 1 includes all groups of three or more males in which practically all fighting was of the exclusive dominance type.

Table 2 contains a series of miscellaneous groups in which many types of order were observed.

Table 4 includes all those in which a fairly definite linear order persisted for a considerable length of time.

Table 5 consists of a few lots of three or more males in which no definite order was established.

Table 6 is a summary of tables 1, 2, 4, and 5.

Table 7 includes all pens of only two males. Some types of orders observed in larger combinations could not possibly occur in these.

To make the results in the tables as objective as possible a set of rigid rules was observed in determining the type of social hierarchy for each group of mice each day. If, for example, one male in a pen was the uncontested victor in all observed contacts for a day he was regarded as the exclusive dominant for that day, regardless of whether on most other days he was a dominant or subordinate animal. Similar definite criteria were used for all categories. Each day's results were classified without any reference to the results of the preceding and following days.

It must be emphasized here that the animals were observed only one to six hours, usually two hours, each day and that many things may have happened in the pen during the time between observations. One may raise the question, then, as to whether the method of sampling of fighting used gives a fair picture for the twenty-four hours.

The fact that in some groups the same male is exclusively dominant day after day and that all of the other males have wounds, where the despot has been seen to bite them, lends strong support to the view that in at least some pens this two-hour sampling of fighting is fair. An additional support of this view is that in some groups the same results are obtained when observations are made for six hours as when they are made for one.

It seems probable, however, that in some other groups the results obtained during two hours of observation are not truly representative of the conditions existing within those groups for

that day. Furthermore, even twenty-four hours of observations a day might not necessarily give a true picture of what would have occurred in the dark or in the absence of the observer.

For each group of males the following information is given in order: (1) the identification number; (2) the number of males present at the beginning of observation; (3) the number of males killed; (4) the number of changes in dominance; (5) the number of days each type of fighting order was observed—columns labeled 1–6 and described in the legend; (6) the number of days fighting occurred but the observer either failed to see the result or the outcome was doubtful, so that it was impossible definitely to classify the order for that day—described as “unknown order” in the tables; (7) the number of days no fighting was seen to occur; and (8) the total number of days of observations.

To illustrate the meaning of the figures in the tables, two examples will be given. The first group (18–B9) in table 1 contained originally three males one of which was killed in the course of the observations. No changes in dominance were observed. Exclusive-dominance type of fighting was seen five days and no fighting two days. Observations lasted seven days. Group 7 in table 2 consisted of three males, none of which was killed by fighting. Distinct changes in dominance were observed four times. An exclusive-dominance order was recorded 120 days; dominance with unsuccessful resistance by a subordinate, 23 days; dominance with no-decision resistance from some males, 2 days; linear order with unsuccessful resistance against the *alpha* male, 4 days; unsettled fighting, 5 days; fighting of unknown order, 11 days; and no fighting, 62 days. The group was observed for a total of 227 days.

Exclusive dominance. By far the most common type of social hierarchy among the observed groups of males is exclusive dominance without resistance. This is classified as type 1 among the categories of fighting orders in the tables. It is well demonstrated in tables 1 and 2. In this kind of social organization one male bites and routs some or all of the other males of the group without any of them fighting back at him or fighting among each other. This condition has persisted for several months

in some pens and in others has been interrupted only occasionally by a few days of other conditions. This is true for all groups

TABLE 1
Groups showing exclusive dominance by one male

GROUP NUMBER	SIZE OF GROUP	MALES KILLED	CHANGES IN DOMINANCE	NUMBER OF DAYS EACH TYPE OF FIGHTING ORDER WAS OBSERVED*								UNKNOWN ORDER	NO FIGHTING	DAYS OBSERVED
				1	2a	2b	3	4a	4b	5a	5b	6		
18-B9	3	1		5									2	7
35-37	4		1	8								2	25	35
44-47	3	2		3										3
49-50	3	1		9			2					2	3	16
73	3			39		1	2							42
75-76	6	5		15								1	2	18
77-78	8	1		47								2	40	89
80-82A	6			35								7	51	93
84	4		1	74						1		2	19	96
89	3			18				1				1	1	28
R1	5	4		31								1	8	48
R3	4		2	60								1	4	87
R2-R3	3	2		3								1		4
Ry	6			10										10
IC	5			5								1		9
ID	5	1		11								1		4
B	3	1	1	49									15	64
Ly2	5	1		13			3					1	4	21
Ly1	4			41			5					6	38	90
Total....	83	19	5	476		1	12	1		1		6	38	803

* Types of fighting order:

1. Exclusive dominance.

2a. Dominance with unsuccessful resistance by a subordinate.

2b. Dominance over some, with no-decision resistance from others.

3. Linear order of dominance with no resistance against the *alpha* male.

4a. Linear order of dominance with unsuccessful resistance against the *alpha* male.

4b. Linear order of dominance with no-decision resistance against the *alpha* male.

5a. Equal dominance with no fighting between equals.

5b. Equal dominance with no-decision combats between equals.

6. Unsettled fighting.

listed in table 1 and some of those in table 2. The difference between the groups listed in table 1 and table 2 is that in the

latter, in addition to exclusive dominance, several other types of social order were seen occasionally.

In 14 of the 19 cases in table 1 the same individual remained dominant throughout the period of observation and in a 15th

TABLE 2
Groups showing a variety of types of fighting order

GROUP NUMBER	SIZE OF GROUP	MALES KILLED	CHANGES IN DOMINANCE	NUMBER OF DAYS EACH TYPE OF FIGHTING ORDER WAS OBSERVED*										UNKNOWN ORDER	NO FIGHT- ING	DAYS OB- SERVED
				1	2a	2b	3	4a	4b	5a	5b	6				
7	3		4	120	23	2		4				5	11	62	227	
13	5		14	114	18	5	5	5		3	3	15	23	43	234	
17	9			81	11	6	2	2	1	2	2	15	70	76	268	
18	4			38			4	1		1		1	5	2	52	
22	7	2	4	102	5	1	5	7				5	13	55	193	
25	3		1	46	7	1		6				5	18	45	128	
28	6	5	1	27	1		11	7		3			6	4	59	
41-43-46	6		7	87	3	4	14	4	2	8	1	5	17	15	160	
56-57-59	8			24	1	2	5	1		2		2	20	7	64	
60-61	3		2	27	2	1	3	1		4	3	6	11	30	88	
63	5		1	32	4		4	3		1		2	6	5	57	
62-63A	5	1	2	9		1	2	1				1		1	15	
62-63B	4	3	1	2			1	1		1					5	
67	4		3	55	7	2	9			1		1	5	34	114	
69	4	1	2	63	7	6	5	8		2		5	14	23	133	
74	3	2	2	41	7	1	13	9	1	1			8	1	82	
85	3			12	2	1	2	3				1	8	28	57	
90	6		2	11	9	3		6		1	1	5	7	4	47	
93	4	1		33			6	3		2			7	12	63	
R2	6			27	4		14	7	1	2		1	13	5	74	
R4	4		8	51	11	5	10	14	3		1	11	9	53	168	
R5	4		5	64	7	3	3	6	2	2	2	5	18	51	163	
R4-R5	5	2		1							1	1			3	
R6	4		2	45	2		7	4		6		1	7	6	78	
IA	6		1	42	1		13			7		1	7	2	73	
D	4	1		15		1	5					4	3		28	
Total....	125	18	62	1169	132	45	143	103	10	49	14	98	306	564	2633	

* See legend for table 1.

case (84) a new despot arose only after the former one was permanently removed. Also in a few groups in some of the other tables only one male ever became dominant.

Litters 84 and 75-76 from table 1 will serve to illustrate this condition. In litter 84 male number 4 was dominant over his three littermates for 76 days, until he was removed. On only one of these days male number 2 likewise routed others and on six days no fighting was observed. Males 1, 2, and 3 had open wounds on their rumps as a result of 4's biting. After 4 was removed 2 arose as despot and remained so. In group 75-76 no-decision fighting was seen on the day the two litters were combined. By the next day male number 2 was dominant and remained so until all the other males were killed by him.

Exclusive dominance but with a different male from time to time as the despot is shown in group R3 in table 1 and in a number of groups in table 2, particularly 13 and 41-43-46. In group

TABLE 3
Number of periods of dominance for each of five males in group 13

MALE	PERIODS OF DOMI- NANCE
No. 11.....	4
No. 10.....	4
No. 8.....	4
No. 6.....	1
No. 2.....	1
Total.....	14

R3, male number 3 was exclusively dominant for 5 days. Then, with no observed no-decision fighting, No. 7 was dominant the next day and remained so for about 70 days. For the first three to four weeks 7 was very severe in his attacks on his three pen mates but gradually became very mild. Eventually No. 2 emerged as despot. In this group, then, three males were dominant at some time, while one was not seen to be dominant at any time.

The many changes in dominance in group 13 are striking. In this pen of 5 males dominance shifted from one individual to another 14 times in $7\frac{1}{2}$ months. Each male was dominant for at least 7 consecutive days, some for several periods, as shown in table 3.

Dominance with resistance. Sometimes an exclusive dominant did not go about unchallenged among the rest of the males. He attacked and routed some or all other individuals. These did not fight among each other but one or more of them fought with the despot. Often the resistant subordinate had both no-decision and losing encounters. This condition is classified as type 2a in the tables. Less often the dominant had only no-decision fights with some members of the group. This condition is classified as type 2b in the same tables. These two types of order are not very common and are probably an expression of incomplete dominance. Certainly they are unstable conditions, for they are seldom observed for more than two or three consecutive days and in most groups are found only in a few widely separate days. Oftentimes they were preceded and followed by many consecutive days of exclusive dominance. Sometimes, however, they occurred between days of other types of social order, or occurred near the beginning of the establishment of a lasting exclusive order.

In some cases dominance with resistance may mean that the domination of the resistant individual by a new despot has not been completed, while in other cases it may mean that the resistant male is breaking away from complete subordination. The appearance of resistance by a heretofore completely subordinate individual may be due to the decline of the dominant or the rise of the subordinate or both.

Linear order of dominance. In this type of social order one particular male is despot over all the other males in the group but one of the individuals subordinate to the first may in turn be dominant over one or more of the others. The despot may be regarded as the primary dominant, or *alpha* male, and the male subordinate to him but dominant over others as secondary dominant, or *beta* male. This type of social order is listed as number 3 in the tables. In a few instances there were several secondary dominants in the same group. And in even more exceptional instances tertiary dominance has been observed. This approaches the "linear" social order common in chickens.

Table 4 contains results from 16 groups of males in which

a fairly definite linear social order was observed for part or all of the period of observation, and one group (54-55) in which equal dominance was found but which is included here for want of a better place to put it. This table, unfortunately, fails to give an adequate picture of the results. From a survey of the daily records it seems quite clear that in these groups there is

TABLE 4
Groups showing a linear arrangement of dominance

GROUP NUMBER	SIZE OF GROUP	MALES KILLED	CHANGES IN DOMINANCE	NUMBER OF DAYS EACH TYPE OF FIGHTING ORDER WAS OBSERVED*									UNKNOWN ORDER	NO FIGHT- ING	DAYS OB- SERVED
				1	2a	2b	3	4a	4b	5a	5b	6			
25-26	5						1	2		1	1	1			6
27-29-30	5			48			20	1		8			17	21	115
52-R27	5	1		9		1	2	3		6	1		3	3	28
52-54	6			19			9	2		1		1	1	19	52
54-55	3	1								3		1			4
62-63	4			32			20	2		1		2	13	17	87
64-65	6		1	39		2	39	16	2	18	2	1	22	9	150
70-71	3		1	19	1		9	2	1	1			4	12	49
72	5		1	39	5	1	22	8	1	14		6	17	3	116
76	4			10			16	2					2	3	33
79	6			21			5	1		7		1	8	27	70
80-81-82B	4			23	1	1	44	9		3			6	7	94
86	3	1	1	17	1		18	14				1	3	3	57
87-88	6		2	26	2		15	10		2		4	8	4	71
96	4	1	1	28		1	9	4	1			3	3	3	52
IB	5			12			29	5	1	2		2	15	7	73
C	5	2	4	109	1		42	14	1	5		5	16	35	228
Total....	79	6	11	451	11	6	300	95	7	72	4	28	138	173	1285

* See legend for table 1.

a more conspicuous linear order than the figures in the table suggest. A better understanding may be promoted by briefly describing the histories of a number of groups.

Group 27-29-30 consisted of 5 males at the time the three litters were combined. No. 29-2 was the undisputed dominant male for the entire period of observation. On only one out of 115 days was he challenged, and then unsuccessfully. But for only two weeks at the beginning of the period and possibly for

a few short periods later was he apparently exclusively dominant. For the rest of the time 30-1, or 30-2, or both, were frequently secondary dominants. No. 29-1, which died in the third week from an unknown cause, and 27-1 at no time were seen biting others.

In group 80-81-82B it seems that No. 4 was primary and No. 3 was secondary dominant for practically the entire period of observation. On 9 out of 94 days, mostly near the end of the period, the latter unsuccessfully challenged the former.

No. 11 in group IB (numbered 7-11) was dominant throughout. On two days he was defeated but on at least one of these days he in turn defeated his victor. On a few other days he was unsuccessfully challenged. No. 7 was never seen fighting; No. 8 and No. 9 were secondary dominants for several days each, and No. 10 was secondary dominant most of the time.

In litter 72 often several, sometimes all 5, males were seen fighting in one day. For 14 weeks this condition continued. Through this entire period No. 4 stood out as the primary dominant. Among the rest of the members there was considerable shifting in position in the social order. On only a very few days was 4 ever attacked or resisted and on even fewer was he defeated, but never completely subordinated. At length, in the 15th week, after two days of unsettled fighting, he lost his position and No. 2, heretofore usually near the bottom of the fighting order, emerged as an exclusive dominant and remained so. The conditions for the first 15 weeks remind one of the "peck dominance" described by Masure and Allee (1934a, b) in pigeons and parakeets.

Group 64-65, with 6 males, was a unique one in that a condition of primary, secondary, and tertiary dominance remained fairly stable for 51 days. This order was not observed every day but often enough to indicate it was there throughout that time. In this hierarchy No. 6 was primary, No. 5 secondary, and No. 2 tertiary dominant. No. 6 often routed all others but sometimes he was resisted by the secondary and once by the tertiary dominant; he was never defeated. The secondary dominant, in addition to occasionally resisting the primary dominant, often

routed all the other members. The tertiary dominant resisted the primary and the secondary dominant each once and frequently routed all other males. Each of the three males at the bottom of the hierarchy routed either the secondary or the tertiary dominant or both a few times. Toward the end of this period No. 5 resisted No. 6 more frequently. Then abruptly No. 6 dropped from his position as *alpha* animal down to the level of males 1, 3, and 4. No. 5 moved from second to first position and No. 2 from third to second. This condition lasted for about 100 days. No. 5 remained at the top all this time but 2 sometimes was routed by those usually subordinate to him.

Linear order with resistance. An *alpha* dominant sometimes was resisted by either a *beta* dominant or a subordinate. Usually in such instances the former was victorious in at least some of the encounters for that day. This is described as type 4a in the tables. In a few instances the *alpha* animal was observed having only no-decision fights with a subordinate. This is type 4b in the same tables. The first of these conditions is not very common and the second extremely rare. Like types 2a and 2b, they seem to be only temporary, unstable conditions.

Equal dominance. Two or occasionally more males were observed routing other males but not each other. They are regarded as equal dominants. If they were not seen fighting each other the condition is classified as type 5a. If they had no-decision fights with each other it is classified as type 5b. These conditions, like 2a, 2b, 4a, and 4b, apparently are only temporary and unstable. One of the best illustrations of equal dominance was group 54-55 in table 2. Unsettled fighting occurred when 54-1 and 54-2 were combined with 55-1. The following three days the two former routed the latter but did not attack each other. So badly was 55-1 wounded that he was killed. The two apparently equal dominants later were combined with litter 52, in which case 54-1 became primary and 54-2 secondary dominant. In many pens apparently equal dominance was observed on a few scattered days.

Unsettled dominance. Fighting in some groups is not always according to a definite order but at times is confused and un-

settled. In one moment a given male may be victorious over his opponent; in the next he may be defeated by the same opponent. In still another moment the same combatants may have a no-decision fight. This unsettled condition may in some cases occur among only a few members of the group, with the rest not fighting at all, while in other cases practically every male participates in confused fighting, each individual attacking the one that happens to be nearest to him.

Unsettled conditions have been observed in many pens, sometimes only on the first day a new group was formed, sometimes on an isolated day in the midst of a long series of days of a definite

TABLE 5
Groups showing no established order

GROUP NUMBER	SIZE OF GROUP	MALES KILLED	CHANGES IN DOMINANCE	NUMBER OF DAYS EACH TYPE OF FIGHTING ORDER WAS OBSERVED*								UNKNOWN ORDER	NO FIGHT- ING	DAYS OB- SERVED
				1	2a	2b	3	4a	4b	5a	5b	6		
24	4			5		2		1		1		6	3	41
52	4			7			1						3	46
56-57	6			14			1			2			8	43
62	3			3						1			2	19
91	6			10		1	8	5		8	2	5	12	61
Total....	23			39		3	10	6		12	2	11	28	210

* See legend for table 1.

order, sometimes at a transition from one order to another, and at times for several consecutive days. Even considering the observed combats only, an unsettled state of affairs was more common than the tables may indicate. Table 5 consists of groups in which no established order was observed but the figures here fail to show the real picture. What actually occurred in these groups was that on one day one male was found routing one or more others, the next day another was the only victor, and on still another day a third individual appeared to be dominant, so that there was no one member that seemed to be consistently superior in fighting among the rest. In group 91 there is an approach toward an order in that male No. 2 was

a victor on more days than any of the others. Still there is no indication of a definite order as was found at some time in most groups.

Group 17 is perhaps the most interesting in this respect. These 7 males were wilder and more difficult to handle than most mice in the colony. A condition of "anarchy" persisted for 105 days, was followed by 42 days of dominance by No. 10, appeared again—this time for 16 days—, and again was followed by dominance by No. 10 for 85 days, until observations were stopped.

No fighting. In most groups no fighting occurred during some observations. This does not necessarily mean that no combats occurred for that day, merely that none was seen during the few hours of observation. In some pens, however, there was no evidence of fighting for periods of many consecutive days. It seems highly probable that in such instances no combats occurred even in the absence of the observer. In some of the groups, periods of considerable fighting were preceded or followed by weeks of peace. Little fighting was observed in very few groups; some combats were seen in each experimental lot. It seems that among those groups in which little or no fighting is seen there are some in which a social order exists and some in which it is lacking. The evidence is: (1) the reactions of the members of a group toward each other, and (2) their reaction to an introduced stranger.

For group 18, which consisted of two males most of the time, both lines of evidence suggest that probably a definite order was present even when no combats were seen. After a long period of fighting in which No. 1 was exclusively dominant there followed a period of 36 days of practically no combats. On each of 4 days during this time No. 1 routed No. 5 once. After this quiet period a strange male, No. B9, was introduced. No. 1 attacked and routed both the strange male and his old littermate, No. 5, but fought the former much more severely. In fact, after 7 days the stranger died, apparently from wounds inflicted by No. 1, whereas No. 5 showed no signs of wounds. Then again followed a period of little or no fighting. In 9 out of 50 days

No. 1 routed No. 5. It is quite possible that No. 1 was always dominant over 5 even when no combats were observed.

Group 6, which consisted of two males, illustrates an apparent condition of no order—or possibly one of equal strength. Fighting between these two males was observed 20 out of 90 days. When it did occur it was mild and infrequent. In 14 of the 20 days fighting was undecided, while on 2 days No. 1 routed No. 2

TABLE 6
Summary of tables 1, 2, 4 and 5

TABLE NUMBER	GROUPS	MALES IN GROUPS	MALES KILLED	CHANGES IN DOMINANCE	NUMBER OF GROUP DAYS EACH TYPE OF FIGHTING ORDER WAS OBSERVED*										UNKNOWN ORDER	NO FIGHT- ING	DAYS OB- SERVED
					1	2a	2b	3	4a	4b	5a	5b	6				
Absolute number																	
1	19	83	19	5	476		1	12	1		1		6	38	268	803	
2	26	125	18	62	1169	132	45	143	103	10	49	14	98	306	564	2633	
4	17	79	6	11	451	11	6	300	95	7	72	4	28	138	173	1285	
5	5	23			39		3	10	6		12	2	11	28	99	210	
Total...	67	310	43	78	2135	143	55	465	205	17	134	20	143	510	1104	4931	
Percentages																	
1			21.7		59.4		0.1	1.5	0.1		0.1		0.7	4.2	33.3		
2			14.4		44.4	5.0	1.7	5.4	3.9	0.4	1.9	0.5	3.8	11.6	21.4		
4			7.6		35.1	0.8	0.5	23.3	7.4	0.5	5.7	0.2	2.2	10.7	13.4		
5					18.6		1.4	4.8	2.9		5.7	1.0	5.2	13.3	47.1		
Mean...			14.0		43.3	2.9	1.1	9.4	4.2	0.3	2.7	0.4	2.8	10.3	22.4†		

* See legend for table 1.

† Days of no observed combat frequently scattered among days of fighting.

without resistance, on 2 days with resistance, and on 2 the outcome was not determined.

Table 6 summarizes tables 1, 2, 4 and 5, which contain data on 67 groups of three or more males. Where possible, the results are expressed both in absolute numbers and in percentages. It shows, as has been stated before, that the exclusive-dominance type of fighting order was observed more often than any other type of hierarchy, that the linear order of dominance is next

in prominence, and that all other kinds of fighting orders are relatively uncommon.

Pairs. Because obviously some types of social hierarchy found in groups of three or more males cannot occur in a pen of only two males, the latter have been summarized in table 7. Here, as in larger groups, complete dominance of one male by another, dominance with resistance, unsettled fighting, periods of no

TABLE 7
Conditions found among pairs of males

GROUP NUMBER	MALE KILLED	CHANGES IN DOMI- NANCE	COMPLETE DOMI- NANCE	RESIST- ANCE TO DOMI- NANT	UNSET- TLED FIGHTING	UN- KNOWN ORDER	NO FIGHTING	DAYS OB- SERVED
6			2	2	14	2	70	90
18			21			4	80	105
22	1	1	6		2		21	29
24		1	17	4	5	4	14	44
26		2	35	3	5	6	46	95
30-			14	1			7	22
44-45	1	1	10			2	3	15
47			8				18	26
54			15	1		4	50	70
60-61	1		5			1	7	13
70-71			37	2		2	40	81
73	1		26			3	12	41
78			22			1	13	36
83			56			7	11	74
86			12	5			1	18
A			69		1	2	12	84
B			25				14	39
Ly1			19			2	44	65
Total...	4	5	399	18	27	40	463	947

fighting, and changes in dominance have been found. The total number of days of no observed fighting is relatively much higher for pairs of males than for larger groups. This by no means necessarily shows that fighting is less common in small groups than in large ones, for in some pairs fighting is as severe and frequent as in larger combinations. In fact, within the range of two to seven males in a group no striking difference in fighting tendency has been observed.

Establishment and persistence of a fighting order

Young males have been seen fighting among each other long before they have attained full size. The average age of 40 groups of mice at the time the first combat was recorded was 50 days. The minimum age at which the first fight was recorded was 30 days and the maximum age was 135 days. In 35, or 87.5 per cent of the groups, this age ranged between 30 and 60 days. These results are shown in table 8. Of these groups most were individual litters while others were several litters of approximately the same age combined. In two cages of combined litters fighting occurred on the day of combination, one at age

TABLE 8
Age at which fighting was first observed in groups of young males

NUMBER OF GROUPS	AGE WHEN FIRST FIGHT WAS OBSERVED
	<i>days</i>
11	30-39
13	40-49
11	50-59
1	60-69
2	70-79
1	117
1	135
40	Average age = 50 days

of 30 and the other at the age of 44 days. In general, it seems that fighting first appears during the second month of age.

Groups vary tremendously not only in the time at which fighting is first observed but even more in the appearance of a definite, well developed social order. In some litters fighting seems to arise rather abruptly with one male as a well established dominant before 60 days of age. In others it seems to develop more gradually, with considerable confusion for several weeks before an order is distinguishable. In groups of strange adult males a definite order usually is apparent within a day or two after the formation of the group. Sometimes fighting is frequent and severe but unsettled; weeks may pass before a definite order

is established. Also, as has been shown before, in groups in which a definite order had once been established and fighting has practically ceased for some time, a new order may suddenly arise or may develop more gradually after a period of unsettled conditions.

Once a definite hierarchy is established it may persist for months without any disturbance; or it may persist for a long time with an occasional disturbance such as several days of resistance, secondary dominance, or unsettled fighting; or it may last for only a few days and then give way to a new order.

Changes in social order

In contrast to groups in which a given hierarchy has lasted for a long time there are others in which the order changes frequently, now one male dominant, now another. These changes in order may, for convenience, be divided into: (1) those occurring without any observed disturbance, and (2) those accompanying or following obvious disturbances of various kinds. The former are much more numerous than the latter.

Changes in the order with no obvious cause sometimes take place very abruptly, occur over night or within the same day without any evidence of an intervening period of unsettled fighting. As has been emphasized before, many things may have happened in a pen during the time between observations. It is possible that some of the changes in the social order which appeared to occur abruptly and without any unsettled fighting actually were accompanied by an unsettled conflict.

More often the changes in dominance are not quite so abrupt but occur more gradually and often are accompanied by some unsettled fighting. For example, in one group a period of exclusive dominance by one male is followed by a long period of unsettled fighting in which practically all males participate. Then eventually one emerges as exclusive dominant.

In another group—or in the same group at a different time—the new dominant arises gradually by resisting the old despot for several days, or by secondarily routing other males and then becoming exclusively dominant. Again, the old despot, after

a period of exclusive dominance may meet resistance by one or more males, other than the "dominant-to-be." Then suddenly the new despot emerges, without himself having had an observed no-decision dispute with the old one. Instead of long periods of unsettled conditions, sometimes there are short unsettled periods of only a day or two. In still another variety, a long peaceful period intervenes between the old and the new orders.

Among the males that have ultimately become dominant were some with big scars on their rumps where they had been severely wounded by despots in some earlier hierarchy.

While most changes in dominance have taken place without any apparent reason, a few have been seen for which plausible causes—not necessarily the correct ones—may be given. One dominant lost his position following the appearance of a large boil-like swelling on his left fore leg. One exclusive dominant and another primary dominant died within two to three days after losing their positions, without any obvious wounds. It is possible that these males lost their place in the order due to illness. Changes in dominance, with the number of observed cases shown in parentheses, followed such disturbances as: 1. Blinding of all males of the group (1). 2. Castration (1). 3. Temporary isolation of the dominant (2). 4. Isolation of all males of the group for a week (1). 5. Exchanging the dominant mouse temporarily for a male from another pen (3). 6. Addition of two strange males (1). 7. Defeat of each male by strange males in other pens (1). Many similar disturbances did not result in changes in dominance. Possibly some changes were directly due to the listed disturbances and others were merely co-incidental to them.

Frequency and severity of fighting among males

The frequency of fights ranges from an isolated observed combat once in a period of several months to many fights per day for many consecutive days. The severity of fighting, too, ranges from a harmless push or snap to bites which cause fatal injuries.

Especially in newly formed groups of strange males very fast

and furious fighting may take place. In some cases one male becomes exclusively dominant at once and charges into the rest, biting them repeatedly and wounding them severely. Within a few days all but the despot are dead from wounds. In other cases severe, free-for-all fighting prevails for a part of a day before one male emerges as the dominant.

Fatal fighting is by no means confined to newly formed groups. It also occurs among littermates and in groups of males that have been together for some time. In group 28, which was composed of 6 littermates, No. 4 was dominant for 50 days. Fighting often was frequent and severe, with 4 exclusively dominant some days but with some secondary dominance many days and some occasional resistance. During No. 4's supremacy two males died of wounds and one was very weak from the same cause. No. 6 then became exclusively dominant and within ten days killed off all the other males in the cage.

Often fighting is frequent and severe without any fatalities. This, like the fatal fighting, occurs especially when a new group is formed, or when a change in dominance takes place, or when a group is disturbed in some way. In some such cases both the frequency and severity of fighting diminish considerably within a week or two; in occasional instances combat ceases altogether. In more cases, however, both the frequency and the degree of severity remain quite high for a month or more, regardless of whether the same male remains dominant throughout that period or several changes in dominance have occurred. Some members of the group may be wounded, usually on the rump or around the genitals.

In a great many groups fighting is more moderate in frequency and severity, with only slight wounding, if any. This condition may remain fairly constant for a long time, while in others both factors may fluctuate considerably and independently. A slight modification of the preceding condition is that in which fighting is moderately frequent but of a very mild character, so that there is no evidence of wounds on any members in the cage. Then, next to no combats at all, there is a condition of very mild and infrequent fighting.

No relationship is apparent between the size of the group and the frequency and severity of fighting, for all degrees have been observed in lots of all sizes from two to seven males.

Generally the dominant male fights all of the subordinates about equally. Very definite exceptions occur, however, as for example in group Ry, where the dominant male repeatedly attacked No. 4 and wounded him but was not seen attacking the three other males. In at least two other groups discrimination was definitely evident.

Space relations between dominant and subordinates

In most cages, even in some when fighting is very severe, all animals cuddle up in the same corner of the pen. In a few periods of severe fighting, however, the dominant male was seen to rest in a corner alone, away from the rest of the group. This is usually associated with the beginning of a new order and seldom lasts for more than a few days, though in some cases the dominant mouse rested alone for three weeks or more. One particular despot occupied the corner ordinarily used by the entire group while the subordinates cuddled in the feed dish. In most other pens the subordinates occupied the usual corner while the despot used another. A primary dominant in one cage was seen usually alone in one corner while the secondary dominant piled up with the rest.

In pen R3 where the *alpha* mouse occupied the nest and the subordinates rested in the feed dish, the isolation of the former was obviously due to the fact that he attacked any of them that came near him. When he was at the feed dish he seldom tolerated them near. In the other pens where the subordinates occupy the nest while the despot remains alone, and both the former and the latter may be found at the feed dish at the same time, the explanation is not so obvious. In the unusual instance of R3 the subordinate males avoided the dominant but in these other cases the despot apparently avoided the subordinates!

Correlation of the social order with other factors

Questions that have been very much in the foreground throughout this study are "what makes a given animal dominant over

another?" and "is success in fighting correlated with anything else?" Neither of these questions has been satisfactorily answered. The fighting order has been compared with such factors as weight, age, copulation order, and reaction to introduced males.

Weight. In an attempt to determine whether there is any correlation between social order and the weight of males, each male in the colony was weighed on two separate occasions. In a number of groups each member was weighed at least once a week for several months. There was no strong correlation between social order and weight, for in one group the dominant mouse was the lightest member, in another he was somewhere in the middle of the weight order, and in a third he was the heaviest animal present. Also changes in dominance occurred without correlated changes in weight. According to statistical analyses, the dominant males tend to be among the heavier and intermediate members of the group more often than among the lightest. In group 28, in which fighting was so severe that all but one male died of wounds, the old dominant was second and the new dominant fourth (last) in the weight order both before and after the shift in dominance. While these data seem to show that position in social order is not highly correlated with the relative weight of each member, observations on temporarily paired males seem to indicate that in some encounters size or physical strength may be a decisive factor but in others it is not. In at least one such instance both males fought very hard and long, and only after repeated severe no-decision fights did the smallest member lose, apparently completely exhausted by the larger male. Often combats between two strange males are decisive long before either is exhausted. In one pair the smallest male may give up, but the opposite result is just as likely to happen.

Age. Age as a factor in determining the social position of a male is eliminated from almost all groups listed in the tables since many of these were single litters and the composite groups consisted usually of males of approximately the same age.

When immature and adult males were temporarily paired in a pen new to both, the adult usually defeated the young male, or no fighting took place. In group 52 two males, from the

age of 69 to 90 days, were occasionally temporarily paired with males 85 days their senior, and were defeated by the latter, while two other males of group 52 were paired with two adults 78 days older, and no fighting was observed. In group 85 several males, from the age of 53 to 79 days were occasionally temporarily paired with males 60 or more days their senior. In 11 instances the younger male was defeated, in one instance no fighting occurred, and on two occasions the young male at the age of 53 days fought no-decision fights with the older animal. In group 91 at the age of from 34 to 66 days the young males were defeated in 13 instances and unmolested in 9 instances by males 20 or more days older.

Mature males have been added to groups of young males. At the ages of 47, 52, 57, 58, and 74 days respectively, members of five groups of young males defeated temporarily introduced mature males who were dominant in their own pens. In one litter 40 days old and in another 51 days of age, introduced adults routed the young.

In these observations there is a very wide range in the age of the young males at which they successfully fight with fully adult individuals. Perhaps a great many more animals would need to be studied to determine the approximate stage at which the age difference between two males is of little or no importance in deciding the outcome of an encounter. Careful distinction would also have to be made between mere size or physical strength differences and the stage of the development of the fighting tendency.

Copulation order. Except sometimes in a group having very rigid exclusive dominance, there is no correlation between the fighting order and the copulation order. In a few instances only the dominant male was observed to mount a female. In almost as many instances only a subordinate male was seen copulating. In most cases several males, dominant and subordinates alike, mounted a female in the same period of observation. In rare instances excited males mounted other males. In one situation in which only the dominant male mounted a female, the subordinates were so strongly negative to the despot that they

rarely ventured from the nest while he walked about. On a few occasions a subordinate mounted a female even in the immediate neighborhood of a strong dominant.

Reaction to introduced males. When a strange male is introduced into a group of males, any one of a number of things may happen: 1. All may attack and defeat him. 2. Only one may rout him. 3. He may attack and rout all of them. 4. No-decision fighting may take place. 5. No fighting may occur. The introduction of a strange male into various sorts of social organizations has given interesting results.

In the majority of instances the introduced male was defeated. The reaction of the old members of the group seems to depend somewhat on the kind of fighting order present at the time. In groups where rigid exclusive dominance prevails, usually only the dominant attacks the introduced male. When the order is less definite, often several or all males attack the new animal. It seems probable that by merely adding a strange male to a pen one can in many instances determine whether a rigid exclusive dominance order is present, and if such an order is there, which male is the exclusive dominant. Exceptions have been noticed, however. So, while there seems to be some correlation between the social order and the reaction of the males to a strange individual, it is not complete. When a strange male was introduced while the dominant was temporarily absent, in some instances the subordinates routed the strange male, in others the latter routed the former, but in most such situations no fighting occurred. Then when the despot was returned he usually attacked and routed the strange male. One might expect that in the absence of the dominant mouse the subordinates would at once attack any intruder. While this occurred a few times, more often it did not. Possibly the removal of the despot a day before the introduction of the strange male would alter the reaction of the subordinates to the latter.

Recognition

Whether a white mouse can always distinguish every individual from any other one in his group is not clear. The reaction of

practically every member in a group to a newly introduced mouse clearly indicates that they can distinguish between an old member and a newly introduced one. Furthermore, the discrimination displayed by the despot against one particular subordinate in a few groups, and a few occurrences of what appeared to be actual avoidance of the primary by the secondary dominant indicate that there is some recognition of old residents of a group. But it seems doubtful whether one mouse always distinguishes between the other mice in the cage. Rather, it sometimes appears as though the subordinates do not recognize the dominant but merely flee from any mouse that happens to attack them or that assumes an aggressive attitude.

Assuming that a mouse recognizes another one in the group, there arises the question as to how he does it. Does he recognize him by sight, smell, bodily movements, or some other means? The analysis of this problem is barely started. So far only the rôle of vision in the reactions of white mice to each other has been studied to some extent.

In five groups of males the animal at the top of the order was discolored with irregular black spots on many places. No changes in the social order occurred. It is quite possible that while the discolored animal looked strikingly different to the observer than it did before, to the subordinate mice the discoloration was insignificant. They might possibly recognize him by his form or odor or in some such manner.

Animals were then blinded to see what effect this would have on their reactions to each other. In one lot of four males having an exclusive dominance type of order a shift of dominance occurred after all were blinded, but the dominance remained exclusive as before. In a group of three males in which likewise an exclusive dominance condition was present, the despot and one subordinate male were blinded. The hierarchy continued as before blinding. After five days the subordinate with intact eyes died of wounds and the old dominant continued routing the subordinate blind male. After a month dominance shifted and the erstwhile subordinate eventually killed his former despot. In a pen of four males in which a definite linear social hierarchy

existed, the primary and secondary dominants were blinded. No change in order occurred. A group of six males in which unsettled fighting prevailed was blinded and the unsettled state of fighting continued.

In their reactions to strange males these blind mice behaved much like males with intact eyes. In an unfamiliar cage some of the blind males, however, appeared to move about slightly more hesitatingly than normal ones. Also they sometimes appeared to approach another mouse more closely before showing any reaction toward it. Otherwise no differences were noticed between the behavior of blinded and normal males.

It seems quite clear then that vision is not essential in the reaction of white mice to each other. If the eyes are intact, however, vision may possibly play a very definite rôle in the recognition of the different members of the group. At least this possibility is not precluded by the foregoing experiments.

The great amount of sniffing among the mice strongly suggests that smell and possibly the vibrissae play important rôles in the inter-reactions of these animals. The destruction of these sense organs may throw some light on the problem of how mice recognize each other.

Effects of castration

In an attempt to study the effect of castration on the fighting tendencies of males some or all males of eight groups of various ages were castrated. Two representative groups will be described briefly before the results will be summarized.

Five adult males from three different pens were castrated and combined in one cage. A regular exclusive dominance order persisted for 11 days. At 40 days after castration a normal male was added. A castrate routed him for 6 days, then followed a long period of no fighting. On 6 days between 156 and 168 days after castration, a castrate fought temporarily introduced normal males. On the 206th day after castration a castrate lashed his tail and apparently fought with an introduced normal. At the 292nd day the group was combined with another lot of castrates. On the day the two groups were combined a cas-

trate of the former fought with the unilateral castrate of the latter group.

A group of males was castrated at 35 to 43 days of age, seven completely castrated, one unilaterally castrated, and one operated but no gonads removed. No fighting was observed among the bilateral castrates, but both the unilateral castrate and the normal male attacked introduced normals and fought with each other a few times. At 247 and 255 days after castration a castrate fought with a strange normal male.

In summary of all the work with castrated males, four groups were castrated after reaching sexual maturity and four before. In two of the former groups all males were completely castrated and in the six others one or more males still retained at least one gonad. In three of the four groups castrated at maturity a castrate was exclusively dominant for some time and in one the uncastrated male was dominant. In three of the four groups castrated before maturity, fighting was very rarely observed and in one a unilateral regularly routed another unilateral castrate. Littermates of castrates of three of the last groups were not operated but were used as control groups; in all these fighting was common; in one all males but one were killed by fighting.

The almost complete absence of fighting among the early castrates, as compared with the frequent fighting in their uncastrated littermates and with the continuation of fighting for a considerable length of time in the late castrates, may be significant.

In three of the late castrated and in two of the early castrated groups a castrate has been known to fight at least as late as 100 days after castration, in one group 292 days after castration. The fact that a few castrates fight, whether castrated before or after reaching maturity, shows that castration does not completely inhibit combativeness. Stone (1927) found a similar effect on the mating behavior of 40 male rats castrated after reaching sexual maturity. In some of these rats the mating reaction apparently disappeared very shortly after castration, while in some it persisted as late as eight months. The fact that in some of the castrate groups the unilateral castrates and

the uncastrated control, as well as occasional groups of normal males, have shown little tendency to fight emphasizes the point that lack of combats in the part of the castrates is not necessarily due to castration.

To check on whether castration was complete on the ones that fought, one adult castrate that had frequently been seen fighting was killed and examined, 144 days after castration, immediately after having vigorously attacked and defeated other males. Both testes were gone and the accessories were in a typical castrate condition. Autopsies were performed on other castrates after they died. These too showed the typical castrate condition.

If all uncastrated males were found to fight and if all castrates were observed to cease fighting after a certain length of time after gonadectomy, it would be an interesting matter to inject male hormone into castrates and to study its effect on the behavior of the animals. In such a case one could attribute any results to the injection of hormone. But as the situation is at present it would be difficult to be sure that the results, whatever they might be, are due to the injections of hormone or whether they are entirely independent of them.

Effects of starvation

Because of the possible survival value of fighting supremacy among mice in time of scarcity of food, the effect of partial starvation was studied on two groups containing both males and females. A feeder was devised whereby only one mouse at a time could get food. This was placed in the pen after food had been absent for 12 to 20 hours. This was tried on four consecutive days in one group and on two days in another.

At times some animals showed no reaction to the food. After getting a mouthful of food an animal usually readily gave way to another. Animals that were observed to be subordinate under ordinary conditions here obtained as much food as their dominant, and females appeared as frequently at the feeder opening as the males. There was considerable pawing and pushing among the animals in their struggle to get at the food, but in at least one of these groups no order of supremacy was observed

in this struggle. Possibly in the group where dominance was very severe the despot was more aggressive in trying to get at the food, but even here the subordinates entered the feed hole in the presence of the despot.

"Home cage" effect

Several references have already been made to the reaction of resident mice to introduced ones. Many groups and individuals were observed to see what effect the familiarity of the environment had on the outcome of encounters between strange mice. Individuals were introduced into groups in the latter's home cage. Regardless of his previous experience as a dominant or a subordinate of a group, or a long isolated individual, the introduced male in the majority of cases was defeated by one or more members of the resident group without even putting up any resistance. Occasionally, however, he fought vigorously before eventually giving up; in some cases he became dominant at once or after some struggle; and in some cases no fighting occurred. Similar results were observed when two strange males were temporarily paired in the home cage of the one. When two strange males were temporarily paired in a pen new to both, the results often were different from those observed when they were placed in the home cage of either. In the new pen combats occurred in relatively fewer pairs, and among the instances of fighting there were more cases of both males actually fighting. In the home cage combats occurred in more instances and the resident often was the undisputed dominant from the start.

Further evidence of a marked effect of the home cage on the opponents is the fact that when the combatants were alternately shifted from the home cage of the one to that of the other, a corresponding alternation in the outcome of the encounters occurred, with each male dominant in his own pen in most instances. Even on several occasions when a group and an individual were alternately shifted from the home cage of the former to that of the latter, the single male defeated the entire group in his own cage but was defeated in the home pen of the group. There were some exceptions to these observations, but in a

majority of cases a mouse combined with one or more strangers won in his home territory and lost in his opponent's familiar pen.

There is some evidence that there is a real home cage effect on a combatant irrespective of the presence or absence of familiar pen mates. And there are indications that the presence of familiar cage mates in a strange territory is of little or no support to a combatant. To the eye of the observer and probably also to that of the mouse there is no difference between the pens of two males. To the nose of the mouse, however, there probably is a very definite difference between the two cages.

Fighting between males and females

Fighting between males and females was very rare. Some of the attacks of the former on the latter were concerned with sexual activity, but others apparently were not. Especially when a male fights other males severely he may occasionally attack a female. Sometimes, however, a female routed a male. This usually happened either when a strange male was added and she, like some of the males, attacked him, or when new members of her own sex were added and she in her excitement of fighting them also attacked some of the males. Combats between males and females are usually one-sided, with the one animal biting and the other fleeing. In very few instances, however, vigorous no-decision fights occurred.

Fighting between females

Fighting between females that have been together for at least several days occurs but rarely. On the other hand, it is very common among females newly combined in the same pen. In almost all instances the resident females routed the introduced ones, but in a few instances the opposite has been observed. If several strange females are combined in a cage new to all, fighting sometimes occurs, but apparently less often than in the familiar cage of one member of the group. Sometimes fighting between females is fatal, but more often it is much less severe and practically ceases after several days. This seems to be true whether a female is introduced into a group of all females or a group of

both sexes. When several residents are present either one or sometimes several of them attack the newly introduced female. If several females are added, often all of them are attacked by a resident. Here, as among the males, the home cage seems to have a very definite effect on the reactions of strange females to each other.

DISCUSSION

Some features of this study have been sufficiently discussed in the preceding paragraphs, so that only a few aspects will be further considered here.

In all that has been and will be said, one must remember that in these studies, as has been emphasized before, the mice were together 24 hours a day, except in a few cases, but were observed only a part of this time. Many things may have happened, particularly in transition periods, of which the observer had only a glimpse. The observed behavior in many cases probably was representative of all behavior, but in some the observed and the unobserved behavior possibly were quite unlike.

Confinement of a variable number of mice in a relatively small space is a condition very probably rarely met by this species outside the laboratory. Under natural conditions there are probably much fewer occasions for several adult males to come into close contact with each other. And when conflicts should occur, the defeated animal would probably not be subjected to repeated assaults by the victor, as in small laboratory cages, but could flee effectively from the attacking mouse even though such flight might expose him to attack by other enemies. Even in densely populated corn bins or other food storage places there probably is much more opportunity to escape from an opponent.

The social level of organization of mice obviously is lower than that of many mammals and birds. Nevertheless, a careful study of the inter-reactions of these convenient animals throws some light on the general problems of social behavior and allows comparisons, some of which deserve comment here.

The overt expression of a social organization was as conspicuous in these mice as in most birds and apparently more conspicuous than in some of the mammals mentioned by Schjelderup-Ebbe.

The great variety of social behavior observed in these many groups of mice possibly throws some light on the difference in the observations recorded by Schjelderup-Ebbe and by Allee and Masure on the same species of birds, chickens excepted. In the light of the present studies, it seems quite natural that different flocks of birds of the same species should have a somewhat different social organization. It may well be that in some flocks of shell parakeets a "peck-right" may prevail, while in others a "peck-dominance."

Triangles, quadrangles and other social hierarchies among birds have been described in which a member near the bottom of the social scale in turn dominates the one at the top. A pecks B, B pecks C, and C in turn pecks A. Schjelderup-Ebbe reported having found similar situations among mammals. No such triangular orders were observed in any of these groups of mice. There have been unsettled conditions in which no member of the group went undefeated. In such a situation the males of a group might be arranged in a triangular order for a day. But such a temporary, unsettled condition cannot be regarded as an order.

Murchison suggests, apparently on the basis of the observation of his flock of eleven chickens, that in a small flock an organization involving triangles, etc., will eventually straighten out into permanent straight-line dominance. In some groups of mice unsettled conditions eventually gave way to a stable, definite dominance order. This would correspond to the gradual development of the straight-line dominance Murchison found in his chickens. But in other groups of mice also the converse occurred, in which a definite order broke down into an unsettled condition. An excellent illustration of the reversibility of this process is group 17, in which two periods of highly unsettled conditions alternated with two periods of a definite dominance order.

Schjelderup-Ebbe believes that there are no two animals living together that do not "know" which of them is the dominant and which the subordinate. Mice seem to be an exception to this rule, for in many groups there are several subordinates which show no evidence that each male "knows" which of them is superior or inferior to the other.

Crew and Mirskaia (1931), in an experiment on the effect of

density on the rate of reproduction in mice, reported that sometimes a defeated male was exiled. This is interesting, since in the present study only the despot was ever definitely seen to rest away from the group. There was one group, however, in which an introduced male was attacked by several old residents day after day until he died. He often was driven out of the nest but never completely exiled. Possibly in a larger cage he would have kept away from the old residents and so would have lived longer.

Another fact reported by these authors and pertinent to the present study is the observation that a strange mouse could be introduced more successfully into a large group than into a small one, presumably because it could lose itself more easily in the crowd and so escape injury. Information of this nature in the present study is insufficient to warrant any generalization. Crew and Mirskaia used larger cages and some larger groups of mice; their observations on behavior were incidental to the main object of their investigation. Extended studies of the behavior of larger groups of mice in pens of various sizes would probably provide interesting and pertinent variations from the results obtained in the present study.

The social organization observed in the albino laboratory mouse reminds one of certain types of human social situations. The dominance-subordination relationships between members of human groups are at times readily observed; at other times they may be obscured by various other aspects of human society. When present, dominance-subordination patterns in man may be determined by a larger, more complex set of factors and may be expressed in many more different ways than those in the mouse. It may well be, however, that the dominance-subordination relations of the mouse and of man have much in common. Without taking the comparison too seriously, the fact that mice, among other mammals, have a definite set of such behavior patterns may help explain, but does not justify, a similar social organization in man.

SUMMARY

1. Fighting is very common among male albino mice, rare between the two sexes, and very rare among the females except for a few days after the introduction of a new female.

2. This fighting varies considerably in: (1) intensity, (2) frequency, and (3) in the type of dominance-subordination relationships, even within the same group. Extremes of no fighting and fatal fighting have been observed alike in litter mates and groups of mixed ancestry.

3. The most common type of social hierarchy, as based upon fighting behavior in groups of mice, is exclusive dominance by one male with no fighting or resistance on the part of any of the subordinates.

4. A linear type of social hierarchy with one male dominant over all others and another dominant over all but the first is also common.

5. Other types of conditions are described but these are much less common and many of them are unstable or transitional conditions.

6. Fighting begins among males usually in the second or third month after birth, on the average at 50 days of age.

7. A definite fighting order may develop gradually or may arise in a very short time.

8. Permanency of a given order may vary from a few days to at least several months. Some males were definitely dominant for only one or two days while others were continuously dominant for many weeks.

9. Dominance is not always confined to one or two males of a group. In some groups each male was exclusively dominant in turn. The same male may be alternately dominant and subordinate.

10. Dominant males usually rest in the corner with the other males but sometimes they rest apart from them.

11. Among adult males, little or no correlation is found between the fighting order and such factors as weight, age, and copulation order. Among mixed groups of mature and immature males, age and weight may be of importance in the determination of the fighting order.

12. A high correlation apparently exists between social order and the reaction to newly introduced males. In firmly established orders usually only the dominant attacks the intruder,

while in unsettled or weak hierarchies several or all residents often may attack the introduced male.

13. Blinding does not seriously interfere with the fighting behavior of males.

14. Castration appears to diminish considerably the fighting reactions of some males but it does not completely inhibit the reaction in all individuals.

15. There seems to be a strong home cage effect on the fighting success of an animal. A male is more likely to win a fight in his home cage than in a strange pen.

16. Certain comparative suggestions are made in the discussion.

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